

阿尔卑斯山高山-亚高山过渡区高山黄花茅 的群体遗传结构和分化研究

¹赵桂仿 ²Francois Felber ²Philippe Kuepfer

¹(西北大学生命科学学院;秦岭生物多样性研究中心 西安 710069)

²(Botanical Institute, University of Neuchâtel, Chantemerle 18, CH-2007, Neuchâtel, Switzerland)

Population genetic structure and differentiation of *Anthoxanthum alpinum* in the subalpine-alpine ecocline of Swiss Alps

¹ZHAO Gui-Fang ²Francois Felber ²Philippe Kuepfer

¹(School of Life Science & Biodiversity Research Center of Mts. Qinling, Northwest University, Xi'an 710069)

²(Botanical Institute, University of Neuchâtel, Chantemerle 18, CH-2007, Neuchâtel, Switzerland)

Abstract Allozyme variation in 6 enzyme systems coding 10 loci was estimated for 18 subpopulations of *Anthoxanthum alpinum* from three altitudinal transects in two localities of the Swiss Alps. Mean proportions of polymorphic loci (95% criterion), average number of alleles per locus, and mean expected heterozygosity were 64.9%, 2.37 and 0.252, respectively. Mean genetic distance among populations was 0.011, and 79% of the genetic variation resided within populations. Based on allozyme analysis, marginal subpopulations appeared to have similar level of genetic variability to central subpopulations. Relatively high genetic differentiation, low gene flow values and small neighbourhood sizes suggested that inbreeding followed by genetic drift was possible causes of low genetic variability in Arpette *A. alpinum* populations.

Key words *Anthoxanthum alpinum*; Allozyme; Genetic structure; Alps

Plant populations are often genetically subdivided on a local scale as the result either of spatial variation in heterogeneous environments or of local gene flow (Handel, 1983; Brown, 1979; Endler, 1977; Levin, Kerster, 1974; Bradshaw, 1972). Restricted gene flow may permit local adaptation (Slatkin, 1985; Dickinson, Antonovics, 1973; Jain, Bradshaw, 1966) and foster genetic isolation by distance (cf. Galen *et al.*, 1991). High levels of gene flow can counteract the action of selection by reducing genetic differentiation among populations (Jain, Bradshaw, 1966). Population differentiation in response to small-scale environmental heterogeneity in microclimate, edaphic and biotic factors has been shown for morphological as well as allozyme traits in natural populations of several plant species (cf. Galen *et al.*, 1991).

Anthoxanthum alpinum Löve & Löve (Poaceae) is a perennial plant. Individuals of this species are diploid ($2n = 10$), predominantly outcrossing because of its self-incompatibility (Zeroual-Humbert-Droz, 1995). *A. alpinum* extends continuously from 1700 m to the highest ridge tops (2800 m) at our study sites in Valais in Swiss Alps. At lower elevation, *A. alpinum* is replaced by

a closely related species, *A. odoratum* ($2n = 20$) (Felber, 1988, 1986). Timberline elevations are at 2200 m for Arpette, and at 2000 m for Belalp, respectively. This allows the study of subpopulations growing in a range of microsites from exposed alpine locations to more sheltered areas at tree line on a large altitudinal gradients (1000 m). However, until quite recently no information is available on microgeographical differentiation in *A. alpinum* populations. Therefore, the objective of this study is to test for genetic structuring of the population of *A. alpinum* by use of *F*-statistics (Wright, 1969, 1921) and to assess genetic differentiation in 18 subpopulations along three altitudinal transects from two localities in Swiss Alps.

1 Materials and methods

1.1 Plant materials

Two sites on siliceous rocks, Arpette and Belalp, were selected in the Swiss Alps (Valais). The two sites are 77 km apart. Arpette is located above Martigny in the Val d'Arpette, in the eastern part of the Mont-Blanc massif, on the left bank of the Rhone valley. In this site, one gradient was set up on the southern slope of the "Clochers d'Arpette" between 1830 m to 2780 m. Distance between the bottom and the top of the gradient is about 1.2 km. The second site, Belalp is situated in the southern part of the Aar massif, in the Aletsch region, on the right side of the Rhone valley, where two gradients were set up on an eastern slope. One is located on Hofathorn between 2020 m and 2830 m (Belalp-1) for a length of 1.75 km. The other ranges between 1815 m and 2550 m, on Foggenhorn (Belalp-2). Its length is of 1.3 km. The horizontal distance between the two gradients of Belalp is about 2.2 km.

At Arpette, the distribution of *A. alpinum* is discontinuous in the forest below tree line (2200 m), where it is restricted to open areas. The population is then continuous in the meadows and the heathes is located between 2200 m and 2600 m, although variations in density occurred. Above 2600 m, *A. alpinum* has a patchy distribution as a consequence of the rocky areas and cliffs. Vegetation of Belalp consists of pastures, meadows and heathes where *A. alpinum* grows in a more or less continuous community.

On each gradient, subpopulations were sampled every 200 m altitude intervals. In 1993, five subpopulations were collected on the gradient of Arpette and four on the gradient of Belalp-1. Sampling was completed in 1994 with two additional subpopulations at Arpette (2620 m and 2780 m). Moreover, the subpopulation of Arpette at 2200 m was collected for the second time (Arpette 2200-B). At Belalp, the subpopulation at 2830 m of Belalp-1 was sampled. Finally, the gradient of Belalp-2 was collected in its totality.

Each subpopulation consisted of 50 ~ 80 individuals collected at a distance of at least one meter from each other. The only exception was the subpopulation of Arpette at 2780 m, where only a few plants (36 individuals) were found. The lowest subpopulation was close to the limit with *A. odoratum*. The highest one was located just below the crest of the mountain. Therefore, the subpopulations sampled at highest and lowest elevations were considered as marginal. The plants were collected and then cultivated in the experimental garden of the University of Neuchatel.

1.2 Electrophoresis

For the extraction of soluble proteins, fresh leaf tissue collected from plants cultivated in the experimental garden was ground at 4°C in 500 ml extraction buffer {0.1 mol/L Tris-HCL, pH7.5, 0.1 mol/L thioglycolate sodium, 0.7% (w/v), polyethyleneglycol 20,000} (Zeroual-Humbert-Droz, 1995). The crude homogenates were centrifuged at 1200 g for 20 min at 4°C. The supernatants were collected and then stored at -80°C.

Electrophoresis was carried out on horizontal starch gels (12%) and on vertical polyacrylamide gels (9%). Histidine-citrate buffer system was used in the starch gels for electrophoresis separation of malate dehydrogenases (E.C. 1.1.1.37, MDH), phosphogluconate dehydrogenases (E.C. 1.1.1.44, PGD), peroxidases (E.C. 1.11.1.7, PX), and alcohol dehydrogenases (E.C. 1.1.1.1, ADH) [electrode buffer: 0.065 mol/L L-Histidine/0.007 mol/L Citric acid, pH 6.5; gel buffer: 0.0162 mol/L L-Histidine/0.00175 mol/L Citric acid, pH 6.5; migration: 20 min at 25 mA/100V, 4 h at 60 mA/300V and 2 h at 40mA/200V] (Zeroual-Humbert-Droz, 1995). PX migrating to the anode (APX) as well as PX migrating to the cathode (CPX) were considered. Glycine-Tris buffer system was used for electrophoresis separation of glutamate oxaloacetate transaminases (E.C. 2.6.1.1, GOT) and tetrazolium oxydases (E.C. 1.15.1.1, TO) in the vertical polyacrylamide gels [electrode buffer: 0.1 mol/L Glycine /0.007 mol/L Tris, pH 8.6; migration: 3 h at 160 mA/600V] (Zeroual-Humbert-Droz, 1995).

Enzyme staining was performed according to the methods described by Wendel and Weeden (1989). In general, substrate concentrations had to be adjusted in respect to the original methods.

Zymograms were analysed according to Zeroual-Humbert-Droz (1995). When one locus coded for several alleles, the slowest-migrating allele was designated as allele a, the others, in turn, were b, c, d up to e according to the number of alleles.

1.3 Data analysis

Allozyme diversity was estimated for each subpopulation by using computer program BIOSYS-I (Swofford, Selander, 1989). The distribution of genetic variation within and among the subpopulations was analysed by the use of F -statistics (Wright, 1969, 1921) with computer program FSTAT (Goudet, 1995). The significance of F_{IS} , F_{ST} and F_{IT} was tested with 1000 permutations.

MDH had a banding pattern corresponding to a duplicate locus. It is not comparable to diploid segregation and was therefore excluded from the above analysis in this study.

Based on the coefficient of Nei's (1978) genetic distance, an unweighted pair group cluster analysis was performed using Wagner procedure. MDH (input with gene frequencies) was included in Nei's measures of genetic identity and genetic distance.

2 Results

Ten loci were scored from the six enzyme systems assayed in this study and the genetic interpretation of zymograms according to Zeroual-Humbert-Droz (1995). The proportion of polymorphic loci was similar for Arpette and Belalp-2 ($P = 57\%$) but higher for Belalp-1 ($P = 80\%$). Similar patterns were observed in the mean number of alleles per locus (A) and the mean expected heterozygosity (He) (Table 1).

The total genetic diversity (F_{IT}) calculated on the basis of the 9 enzyme loci and for all subpopulations was 0.271. A large proportion of the total genetic variation (F_{IT}) appeared to be derived from values of F_{IS} (0.249) and only a small amount of differentiation between subpopulations ($F_{ST} = 0.029$). All indices were significant except for the F_{IS} of locus Pgd-2 which was an almost monomorphic locus (Table 2). Based on altitudinal gradients, F_{IT} , F_{ST} and F_{IS} were significant when the data of all the loci were considered. F_{IT} value was the lowest for Arpette (0.231) while Belalp-1 (0.292) showed a higher F_{IT} value than Belalp-2 (0.264). F_{ST} values were of the same order of magnitude at Arpette (0.022) and Belalp-1 (0.020) and the lowest at Belalp-2 (0.013). Inversely, F_{IS} was higher at Belalp-2 (0.254) than Arpette (0.214) and Belalp-1 (0.227) (Table 3).

Table 1 Genetic variability at 10 loci for all subpopulations: mean sample size per locus (N), proportion of polymorphic loci (P), mean number of alleles per locus (A), mean expected heterozygosity (He) and their standard errors (s.e.)

Populations	N (s.e.)	P (%)	A (s.e.)	He (s.e.)
Arpette				
1830	38.7 (0.4)	66.7	2.2 (0.3)	0.240 (0.072)
2015	52.8 (0.5)	66.7	2.4 (0.4)	0.244 (0.074)
2200	71.4 (0.2)	44.4	2.2 (0.4)	0.215 (0.079)
2215	53.7 (1.1)	55.6	2.7 (0.3)	0.237 (0.072)
2415	72.8 (0.1)	55.6	2.4 (0.4)	0.232 (0.072)
2445	64.0 (1.3)	66.7	2.4 (0.2)	0.238 (0.067)
2620	81.0 (0.0)	44.4	2.3 (0.4)	0.202 (0.075)
2780	36.0 (0.0)	55.6	2.0 (0.3)	0.219 (0.079)
overall		57.0	2.3 (0.1)	0.228 (0.026)
Belalp-1				
2020	73.2 (2.9)	77.8	2.8 (0.3)	0.317 (0.063)
2200	77.4 (0.3)	77.8	2.7 (0.3)	0.282 (0.070)
2405	70.1 (2.3)	100.0	2.6 (0.3)	0.326 (0.062)
2575	83.1 (0.9)	88.9	2.3 (0.2)	0.288 (0.060)
2830	74.6 (0.2)	55.6	2.2 (0.4)	0.212 (0.074)
overall		80.0	2.5 (0.1)	0.285 (0.029)
Belalp-2				
1815	69.0 (0.0)	55.6	2.3 (0.4)	0.210 (0.079)
2030	74.0 (0.0)	66.7	2.6 (0.2)	0.261 (0.072)
2230	71.1 (0.4)	55.6	2.3 (0.4)	0.246 (0.080)
2430	62.0 (0.0)	55.6	2.3 (0.4)	0.258 (0.077)
2550	74.0 (0.0)	55.6	2.2 (0.3)	0.246 (0.082)
overall		57.8	2.3 (0.2)	0.244 (0.034)
Mean		64.9	2.37	0.252

Table 2 Summary of F -statistics for 9 loci over 18 subpopulations (* : $p < 0.05$)

Enzyme loci	F_{IT}	F_{ST}	F_{IS}
Got-1	0.199*	0.049*	0.157*
Got-2	0.085*	0.028*	0.058*
To-1	0.399*	0.015*	0.390*
To-2	0.380*	0.016*	0.369*
Pgd-1	0.322*	0.036*	0.296*
Pgd-2	0.123*	0.034*	0.092
CPx-1	0.158*	0.015*	0.145*
Px-1	0.468*	0.012*	0.462*
Adh-1	0.893*	0.040*	0.888*
Overall	0.271*	0.029*	0.249*

The species mean fixation indices (F) varied largely when subpopulations and loci were considered individually. They did not show significant differences between the central and the marginal subpopulations for each altitudinal gradient. Most of F values were positive, which reveals a deficit in heterozygotes. Nevertheless, only few significant deviations from Hardy - Weinberg equilibrium

Table 3 Summary of F -statistics for 9 loci over the three gradients(* : $p < 0.05$)

Enzyme loci	F_{IT}	F_{ST}	F_{IS}
Arpette			
Adh-1	0.664 *	0.003	0.663 *
Px-1	0.453 *	0.020 *	0.442 *
CPx-1	0.260 *	0.015	0.249 *
Got-1	0.140 *	0.031 *	0.113 *
Got-2	0.092	0.015	0.079
Pgd-1	0.076	0.033 *	0.044
Pgd-2	-0.001	-0.001	-0.002
To-1	0.276 *	-0.002	0.277 *
To-2	0.498	-0.004	0.500
Overall	0.231 *	0.022 *	0.214 *
Belalp-1			
Adh-1	1.000 *	0.038 *	1.000 *
Px-1	0.486 *	0.009	0.481 *
CPx-1	0.100	0.012	0.089
Got-1	0.238 *	0.017 *	0.224 *
Got-2	0.059	0.016	0.044
Pgd-1	0.436 *	0.057 *	0.402
Pgd-2	0.116	0.012	0.105
To-1	0.337 *	0.016	0.326 *
To-2	0.160 *	0.011	0.151
Overall	0.292 *	0.020 *	0.227 *
Belalp-2			
Adh-1	1.000 *	0.026 *	1.000 *
Px-1	0.460 *	-0.006	0.463 *
CPx-1	0.094 *	0.027 *	0.069 *
Got-1	0.158 *	0.015 *	0.145 *
Got-2	0.063	0.008	0.055
Pgd-1	0.570 *	0.024 *	0.559 *
Pgd-2	0.000	0.013	-0.013
To-1	0.589 *	0.001	0.589 *
To-2	0.745 *	-0.001	0.745 *
Overall	0.264 *	0.013 *	0.254 *

were noticed (Table 4).

Analysis of Nei's (1978) genetic distance (D) and genetic identity (I) showed that the mean value of genetic distance was 0.011 (ranging from 0 ~ 0.030) and the mean value of genetic identity was 0.989 (ranging from 0.971 ~ 1.000) (Table 5). Despite high genetic identity among the subpopulations, genetic differences in two sampling sites (Arpette and Belalp) were observed in the distance Wagner tree by the cluster analysis (Fig. 1). Based on altitudinal gradient, genetic distance tended to increase with geographical distance (differences of the elevation) between the subpopulations when the crest subpopulation was compared with other ones (Table 5). The correlation between genetic distance and difference of altitude was significant ($r = 0.54$, $p < 0.02$) when all 18 subpopulations were pooled.

Table 4 Fixation indices for each gradient

	ADH-1	APX-1	CPX-1	GOT-1	GOT-2	PGD-1	PGD-2	To-1	To-2	mean
Arpette										
1830	0.843	0.518 *	0.089	-0.171	-0.086	-0.173	-	-0.013	-	0.145
2015	0.651	0.541	0.275	0.065	-0.100	0.122	-	-0.029	-	0.212
2200A	0.794	0.330 *	-0.024	0.143	-0.032	-0.003	-	-	-	0.137
2200B	0.659	0.564	0.165	0.092	0.112	-0.114	-0.010	1.000	1.000	0.206
2415	0.588	0.441 *	0.589	-0.004	0.190 *	0.408	-	-0.028	-	0.313
2445	0.645	0.443 *	0.040	0.184	0.164	-0.071	-0.008	0.659	-0.007	0.196
2620	1.000	0.370 *	0.254	0.134	0.104	-0.052	-	-0.006	-0.006	0.205
2780	-0.043	0.249	0.556	0.323	-0.133	-0.108	-	-	-	0.265
Belalp-1										
2020	1.000	0.553	0.110	0.094	0.206	0.296 * *	-0.024	0.244	-0.049	0.330
2200	1.000	0.593	0.168	0.225 *	0.189	0.413	-0.034	0.358	0.174	0.295
2405	1.000	0.727	0.253	0.205	0.046	0.684	0.209	0.442 *	0.398	0.375
2575	1.000	0.332 *	-0.134	0.317 * *	0.081	0.584	0.148	0.179	0.042	0.238
2830	1.000	0.161	0.020	0.217	-0.169	-0.056	-0.027	-	-	0.093
Belalp-2										
1815	-	0.478	0.115	0.058	-0.100	0.554	-	1.000 *	1.000 *	0.216
2030	1.000	0.753	0.162	0.280 *	-0.098	0.916	-0.021	0.550 *	0.550 *	0.396
2230	-	0.406 * *	-0.076	0.186	0.042	0.640	-	1.000	1.000	0.146
2430	-	0.217 *	0.062	0.006	0.033	0.394 * *	-	0.299	1.000	0.146
2550	-	0.363	0.033	0.120	0.260 *	0.442	-	-0.007	-0.007	0.220

* indicates the probability of departure of Hardy-Weinberg equilibrium. (* : $p < 0.05$; * * : $p < 0.01$)

3 Discussion

A. alpinum is a predominantly outcrossing species (Zerual-Humbert-Droz, 1995). The general prediction for highly outcrossing species is usually relatively homogeneous with alleles uniformly distributed through the populations (Hamrick *et al.*, 1979). Populations of *A. alpinum* in the subalpine-alpine transition zone maintain comparable levels of genetic variability to other outcrossing species. The mean proportion of polymorphic loci in *A. alpinum* is 64.9%, which is higher than the mean value ($P = 51.0\%$) for other outbreeders (Gottlieb, 1981). The mean number of alleles per locus ($A = 2.37$) is somewhat lower than the mean ($A = 2.90$) reported for the outcrossers (Gottlieb, 1981) but higher than the mean ($A = 1.53$) for other plant species (Hamrick, Godt, 1990). The mean expected heterozygosity in *A. alpinum* ($He = 0.252$) is slightly lower than the mean value ($He = 0.29$) for the outbreeders (Gottlieb, 1981) but much higher than the mean ($He = 0.086$) reported for the outcrossing species (Gottlieb, 1981) and the mean ($He = 0.113$) within plant population levels for other plant species (Hamrick, Godt, 1990).

Despite relatively small proportion of genetic differentiation between the subpopulations of this species, there are some obvious differences in the level of genetic diversity among subpopulations. These differences are showed not only by the mean number of alleles per locus (A), the mean values of genetic distance (D) (Table 5), but also by the species mean fixation index (Table 4).

A positive species mean fixation index (F) indicates that there is a considerable excess of homozygotes compared to the expected proportions of homozygote loci. Based on geographical range of

Table 5 Unbiased genetic identities (I) (below diagonal)

	Arpette							
	1830	2015	2200	2215	2415	2445	2620	2780
1830	-	0.011	0.004	0.006	0.009	0.015	0.011	0.015
2015	0.989	-	0.004	0.009	0.004	0.014	0.011	0.008
2200	0.996	0.996	-	0.001	0.004	0.007	0.004	0.004
2215	0.994	0.991	0.999	-	0.004	0.014	0.006	0.008
2415	0.991	0.996	0.996	0.996	-	0.012	0.001	0.003
2445	0.985	0.986	0.993	0.986	0.988	-	0.010	0.004
2620	0.989	0.989	0.996	0.995	0.999	0.990	-	0.000
2780	0.985	0.992	0.996	0.992	0.997	0.996	1.00	-
2020	0.988	0.975	0.985	0.982	0.981	0.991	0.981	0.985
2200	0.980	0.978	0.988	0.985	0.988	0.996	0.991	0.996
2405	0.977	0.971	0.982	0.978	0.980	0.994	0.984	0.990
2575	0.981	0.975	0.985	0.980	0.983	0.997	0.985	0.991
2830	0.976	0.977	0.984	0.972	0.976	0.996	0.980	0.990
1815	0.991	0.978	0.993	0.990	0.990	0.991	0.993	0.994
2030	0.981	0.975	0.986	0.979	0.980	0.992	0.984	0.992
2230	0.991	0.990	0.995	0.988	0.990	0.996	0.989	0.994
2430	0.981	0.979	0.987	0.979	0.981	0.998	0.982	0.991
2550	0.976	0.984	0.986	0.976	0.980	0.995	0.979	0.990

mean genetic distance = 0.011, from 0.000 to 0.030; mean genetic identity = 0.989, from 0.971 to 1.000

A. alpinum, it appeared that there were no differences for F values between marginal and central subpopulations with the exception of the crest subpopulation of Belalp-1 where a low F value was found. In general, marginal situation may be stressful and may therefore be genetically different. Because of developmental instability, breeding system changes and gene flow effects in species margins (Soule, 1973; Mayr, 1963), and because of different measures of genetic variation, previous investigations of comparative genetic properties of marginal and central populations may give conflicting results (Grant, Antonovics, 1978). Some of these studies, for example, supported the basic patterns of decrease in genetic variation near species margins (Soule, 1973), and others found no decrease or an overall increase in genetic variation from allozymes and some quantitative traits (Linhart, 1974; Tigerstedt, 1973). Our allozyme results in this study showed that the marginal subpopulations appeared to have similar levels of genetic variability to the central ones on all three gradients based on the mean proportion of polymorphic loci (P), the average number of alleles per locus (A) and the mean expected heterozygosity (He) with the exception of the crest subpopulation of Belalp-1 where there were lower values of P , A and He .

Gene flow among populations has an important influence on the distribution of genetic variation. Species with restricted gene flow usually exhibit greater genetic differentiation than species with widely dispersed pollen and seeds (Hamrick, 1989). However, even in outcrossing species, gene flow is often quite limited (Hamrick, 1982; Levin, 1981) and disperse over a short distance (Price, Waser, 1979). Such plants are likely to show pronounced microgeographical genetic differentiation resulting from drift in subpopulations isolated by distance or from adaptation to local edaphic and biotic conditions (Schaal, 1974; Jain, Bradshaw, 1966). In this study, gene flow was measured by using the relationship $F_{ST} = 1/(4Nm + 1)$ (Wright, 1951). Nm in this case is amount of

and genetic distances (D) (above diagonal) between the 18 subpopulations

Belalp-1					Belalp-2				
2020	2200	2405	2575	2830	1815	2030	2230	2430	2550
0.012	0.020	0.023	0.020	0.024	0.009	0.019	0.009	0.019	0.024
0.025	0.022	0.030	0.025	0.024	0.022	0.026	0.010	0.021	0.016
0.015	0.012	0.018	0.015	0.016	0.007	0.014	0.005	0.013	0.014
0.019	0.015	0.022	0.020	0.029	0.011	0.021	0.012	0.021	0.024
0.019	0.012	0.020	0.017	0.024	0.010	0.020	0.010	0.019	0.020
0.009	0.004	0.006	0.003	0.004	0.009	0.008	0.004	0.002	0.005
0.019	0.009	0.016	0.015	0.020	0.007	0.016	0.012	0.018	0.021
0.015	0.004	0.010	0.009	0.010	0.006	0.008	0.006	0.009	0.010
-	0.006	0.013	0.011	0.017	0.008	0.008	0.009	0.006	0.016
0.994	-	0.002	0.003	0.009	0.004	0.002	0.004	0.001	0.008
0.987	0.998	-	0.000	0.010	0.010	0.006	0.008	0.006	0.012
0.990	0.997	1.000	-	0.007	0.009	0.006	0.007	0.005	0.010
0.983	0.992	0.990	0.993	-	0.011	0.005	0.006	0.002	0.002
0.992	0.996	0.990	0.991	0.989	-	0.003	0.005	0.007	0.014
0.992	0.998	0.994	0.994	0.995	0.997	-	0.003	0.001	0.005
0.991	0.996	0.992	0.993	0.994	0.995	0.997	-	0.001	0.002
0.994	0.999	0.994	0.995	0.998	0.993	0.999	0.999	-	0.000
0.985	0.992	0.988	0.990	0.998	0.986	0.995	0.998	1.000	-

immigrates per generation. In addition, from the measure of Nm , an approximative amount of neighbourhood size ($Nb \approx 2\pi Nm$) can be also obtained (Slatkin, Barton, 1989), where Nb is the number of individuals which can interbreed. Nm values of about one or less imply that gene flow may be weak enough between populations so that population differentiation may be due to genetic drift and values greater than one indicate relatively extensive gene flow and a limited capacity for genetic differentiation within populations (Slatkin, Barton, 1989). In the case of *A. alpinum*, Nm was 8.4, $Nb \approx 53$. This suggests that the movement of genes in the populations of *A. alpinum* seems to be consistent. This is in agreement with the prediction for outcrossing species.

Moreover, the data from F -statistics were also in accordance with what might be expected from the vegetation structure. At the scale of the gradient, the highest F_{ST} values were observed for Belalp-1 and Arpette, where *A. alpinum* grows on patches at low and high altitudes. Belalp-2 is a gradient with the smallest interval of altitude.

The higher genetic variability in *A. alpinum* populations from Belalp-1 (Belalp-2 is a gradient with too small interval of altitude to compare) compared to those from Arpette could also partly reflect geographical differences resulting from different selection pressures acting in the two habitats. Both localities are located in the Swiss Alps of Valais, but Arpette, in the extreme eastern part of the Mont-Blanc massif, is a narrow side valley, east-west oriented, and located at the crossing of three main bioclimates of the Alps (external, intermediate and inner Alps). In this type of habitat the ecosystems should be quite sensitive to environmental change. While Belalp, in the south part of the Aar massif, is a wide open lateral valley, north-south oriented, belonging to more continental zone of the inner Valis (Theurillat *et al.*, 1998), and the latter may be more suitable for the

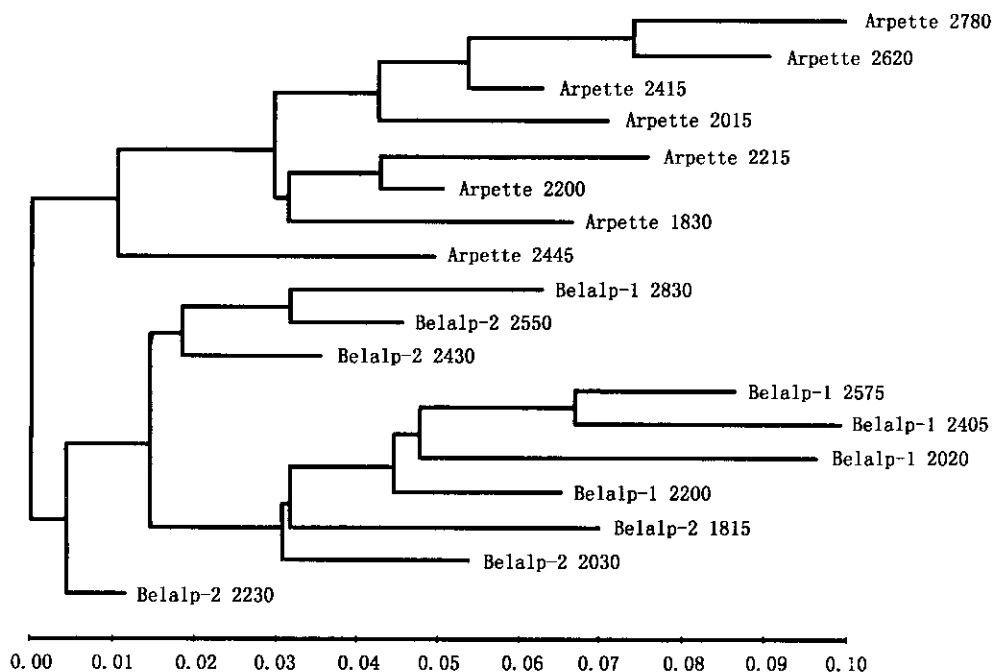


Fig. 1 Dendrogram resulting from unweighted pair group cluster analysis.
Coefficient used: Nei (1978) unbiased genetic distance.

growth and reproduction of this species than the former may be. Therefore, the population of *A. alpinum* in Arpette was likely to fluctuate in response to climate changes because of its poor adaptation to the environment. These factors could have resulted in the disconnected distribution of *A. alpinum* population in Arpette and decreased the effective population size, restricted the movement of genes and therefore increased the impact of genetic drift.

References

- Bradshaw A D, 1972. Some of the evolutionary consequences of being a plant. *Evol Biol*, 5: 25 ~ 43
- Brown A H D, 1979. Enzyme polymorphism in plant populations. *Theor Popul Biol*, 15: 1 ~ 42
- Dickinson H, Antonovics J, 1973. Theoretical consideration of sympatric divergence. *Amer Nat*, 107: 256 ~ 274
- Endler J A, 1977. *Geographical Variation, Speciation and Clines*. Princeton: Princeton University Press
- Felber F, 1986. Distribution des cytotypes d' *Anthoxanthum odoratum* L. s. lat. en Suisse. Les relations Alps-Jura. *Bot Helvetica*, 96(2): 145 ~ 158
- Felber F, 1988. Distribution des cytotypes d' *Anthoxanthum odoratum* L. s. lat. en France et dans les regions Limitrophes. *Bull Soc Bot Fr*, 135, *Lettres Bot*, 131: 281 ~ 293
- Galen L, Shore J S, Deyoe H, 1991. Ecotypic divergence in alpine *Polemonium viscosum*: genetic structure, quantitative variation, and local adaptation. *Evolution*, 45(5): 1218 ~ 1228
- Gottlieb I D, 1981. Electrophoretic evidence and plant populations. In: Reinhold L, Harborne J B, Swain T eds. *Progress in Phytochemistry*. Oxford: Pergamon. 7: 1 ~ 46

- Goudet J, 1995. FSTAT version 1.2: A computer program to calculate *F*-statistics. *J Heredity*, 86: 485 ~ 486
- Grant M C, Antonovics J, 1978. Biology of ecologically marginal populations of *Anthoxanthum odoratum*. 1. Phenetics and dynamics. *Evolution*, 32: 822 ~ 838
- Hamrick J L, Linhart Y B, Mitton J B, 1979. Relationships between life history characteristics and electrophoretically detectable genetic variation in plants. *Ann Rev Ecol Syst*, 10: 173 ~ 200
- Hamrick J L, 1982. Plant population genetics and evolution. *Am J Bot*, 69(10): 1685 ~ 1693
- Hamrick J L, 1989. Isozymes and the analysis of genetic structure in plant populations. In: Soltis D E, Soltis P S eds. *Isozymes in Plant Biology*. Portland: Dioscorides Press. 87 ~ 105
- Hamrick J L, Godt M J W, 1990. Allozyme diversity in plant species. In: Brown A H D, Clegg M T, Kahler A L, Weir B S eds. *Plant Population Genetics, Breeding and Genetic Resources*. Sunderland, Mass: Sinauer. 43 ~ 63
- Handel S N, 1983. Pollination ecology, plant population structure, and gene flow. In: Real L ed. *Pollination Biology*. New York: Academic Press. 163 ~ 211
- Jain S K, Bradshaw A D, 1966. Evolutionary divergence among adjacent plant populations. I. The evidence and its theoretical analysis. *Heredity*, 20: 407 ~ 441
- Levin D A, 1981. Dispersal versus gene flow in plants. *Ann MO Bot Gard*, 68: 233 ~ 253
- Levin D A, Kerster H W, 1974. Gene flow in seed plants. *Evol Biol*, 7: 139 ~ 220
- Linhart Y B, 1974. Intra-population differentiation in annual plants. I. *Veronica peregrina* L. raised under non-competitive conditions. *Evolution*, 28: 232 ~ 243
- Mayr E, 1963. *Animal Species and Evolution*. Cambridge, Mass: Belknap Press
- Nei M, 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics*, 89: 583 ~ 590
- Price M V, Waser N M, 1979. Pollen dispersal and optimal outcrossing in *Delphinium nelsonii*. *Nature*, 277: 294 ~ 297
- Schaal B A, 1974. Isolation by distance in *Liatris cylindracea*. *Nature*, 252: 703
- Slatkin M, 1985. Gene flow in natural populations. *Ann Rev Ecol Syst*, 16: 393 ~ 430
- Slatkin M, Barton N H, 1989. A comparison of three indirect methods for estimating average levels of gene flow. *Evolution*, 43: 1349 ~ 1368
- Soule M, 1973. The epistasis cycle: A theory of marginal populations. *Ann Rev Ecol Syst*, 4: 165 ~ 188
- Swofford D L, Selander R B, 1989. BIOSYS-1——A computer program for the analysis of allelic variation in Population Genetics and Biochemical Systematics. Release 1.7. Illinois: Illinois National History Survey
- Theurillat J P, 1998. Sensitivity of plant and soil ecosystems of the Alps to climate change. In: Cebon P, Dahinden U, Davies H C *et al.* eds. *Views from the Alps——Regional Perspectives on Climate Change*. Cambridge, Mass & London: The MIT Press. 225 ~ 290
- Tigerstedt P M A, 1973. Studies on isozyme variation in marginal and central populations of *Picea abies*. *Hereditas*, 75: 47 ~ 60
- Wendel J F, Weeden N F, 1989. Visualization and interpretation of plant isozymes. In: Soltis D E, Soltis P S eds. *Isozymes in Plant Biology*. Portland: Dioscorides Press. 5 ~ 45
- Wright S, 1921. Systems of mating. *Genetics*, 6: 111 ~ 178
- Wright S, 1969. *Evolution and the Genetics of Populations*. Vol 2. *The Theory of Gene Frequencies*. Chicago: University of Chicago Press
- Zeroual-Humbert-Droz C, 1995. Interaction reproductives entre *Anthoxanthum alpinum* diploïde et *Anthoxanthum alpinum* tétraploïde: conséquences sur la structure génétique des populations pures et mixtes. Ph. D. Thesis, Switzerland: University of Neuchâtel

摘要 应用等位酶分析,在瑞士阿尔卑斯山的阿尔拜特(Arpette)和拜阿尔普(Belalp),沿三个不同的海拔梯度,研究了高山黄花茅3个自然居群的遗传变异和分化。研究结果表明,平均的多态性位点比例为64.9%,每个位点平均等位基因数为2.37,平均期望杂合性为0.252。亚居群间平均的遗传距离为

0.011,发现 79%的遗传变异存在于居群内。基于等位酶分析,边缘亚居群与中心亚居群似乎有类似的遗传变异性。相对比较高的遗传分化、低的亚居群间基因流和小的邻居大小值暗示,近交和随后的遗传漂变可能是导致阿尔拜特黄花茅居群遗传变异性较低的主要原因。

关键词 高山黄花茅;等位酶;遗传结构;阿尔卑斯山

(责任编辑 白羽红)

《植物分类学报》2000 年编委会会议纪要

在《植物分类学报》即将迎来创刊 50 周年纪念日之际,我刊于 2000 年 10 月 20 日召开了京区编委会。13 位编委和编辑部 3 位编辑出席了会议。会议由主编杨亲二主持,主要讨论如何进一步提高刊物质量及为创刊 50 周年特刊征稿等问题。

首先由编辑部介绍了本刊的办刊情况。据不完全统计,1996~2000 年期间,我刊发表的论文涉及相关项目获奖者达 64 篇次;本刊在“1994~1998 年被引频次最高的 500 种中国科技期刊”中排名第 39 位;被国外 11 种、国内 8 种检索系统和数据库收录。平均发表周期约 11 个月。同时,我们也清醒地认识到了目前办刊的不利因素。众所周知,由于种种原因,近年来国内学者趋向于将研究成果投向国外刊物或国内一些综合性较强因而影响因子较高的刊物发表,这给本刊来稿的数量和质量带来一定影响。面对国际和国内竞争,编委们提出了以下建议。

1. 加快出版周期,一般稿件一年内出版,两审都认为非常优秀的文章可更快发表;增加快讯、简报专栏。
2. 由于分类学是一门无穷综合的学科,今后可更多发表与系统进化植物学相关的多学科论文。
3. 请求每位编委每年为本刊撰写或推荐 1 篇优秀论文。
4. 刊登全年审稿人姓名,向审稿人致谢。
5. 为扩大宣传并获取信息,可考虑聘请通讯编委;争取多请国外专家审稿,向国外约稿;在国外著名相关网站建立本刊主页,刊登英文的刊物简介和征稿简则。
6. 向主办单位领导呼吁重视植物分类学研究,取得主办单位的支持。
7. 加强编辑工作:为缩短刊期,请求审稿专家审阅时间最长不超过 15 天;编辑部在作者投稿 3 个月以内告之能否录用;提高编辑素质,认真执行编辑工作程序,提高编辑工作质量,加强现代化管理。

就出版创刊 50 周年纪念特刊一事,编委们也进行了认真讨论,同意在 2001 年出版 1 期纪念特刊。最后,编委们一致认为,我国拥有种类十分丰富的植物区系,亟待研究的分类学问题还很多,应当而且能够办好一本已有 50 年历史的专业期刊。我们一方面要对目前办刊的不利因素有清醒的认识,正视工作中的不足之处,但同时也不宜妄自菲薄。本刊应树立为国家科学发展而不断努力的坚定理念,脚踏实地,埋头苦干,以严谨求实的科学态度和对国家、主办单位、作者、读者高度负责的精神对待每一篇稿件,争取作者的理解和支持。相信随着国家经济和科学技术的不断发展及我国植物分类学家整体素质的不断提高,本刊最终将走出困境,跻身于国际优秀期刊之列。

本刊编辑部